Blister-Rust-Resistant Western White Pines for British Columbia

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Cover image: orange aeciospores outline the diamond shape of a blister rust canker on western white pine.

Abstract

White pine blister rust, caused by *Cronartium ribicola* J.C. Fisch., is a fungus disease originally introduced to British Columbia from Asia via Europe. It attacks all white pines, both native and introduced. It is particularly devastating to native pines because they have little or no resistance to the fungus. For many years, western white pine, a high-value native species with desirable wood and silvicultural properties, was not managed because of this disease. Research in British Columbia has demonstrated how wild stands can be managed and has provided blister rust resistant clones for seed orchards. This report summarizes white pine disease management and how resistant clones were identified for reforestation programs in British Columbia.

Résumé

La rouille vésiculeuse du pin blanc est une maladie causée par le *Cronartium ribicola* J.C. Fisch., champignon d'origine asiatique introduit d'Europe en Colombie-Britannique. Toutes les espèces de pins blancs, tant indigènes qu'introduites, sont vulnérables. Les espèces indigènes sont cependant plus durement touchées, car leur résistance au champignon est dans le meilleur des cas très faible. Pendant de nombreuses années, le pin argenté, essence indigène de grande valeur appréciée pour la qualité de son bois et ses propriétés sylvicoles, n'a pas été utilisée à des fins d'aménagement en raison de sa vulnérabilité à la maladie. Des recherches effectuées en Colombie-Britannique ont conduit à la découverte de nouvelles options de lutte contre la maladie dans les peuplements sauvages et à la mise au point de clones résistants à la rouille vésiculeuse pour les vergers à graines. Ce rapport décrit brièvement les diverses options de lutte contre la rouille vésiculeuse du pin blanc et indique comment les clones résistants ont été choisis en vue des programmes de reboisement en Colombie-Britannique.

Introduction

Western white pine, *Pinus monticola* D. Don, has a white wood that is easily worked, takes paint uniformly and is traditionally used for furniture, sash and pattern making. Therefore, it commands high values and traditionally generates high provincial government revenues (Muir and Hunt 2000). It is also silviculturally desirable because it is resistant to root rots (Nelson and Sturrock 1993; Morrison and Mallett 1996) and grows rapidly. The lumber can be a substitute for eastern white pine (*P. strobus* L.), thus relieving the pressure to cut eastern white pine, which is ecologically important for bear habitat and raptor perching (Rogers and Lindquist 1992).

Originally from Asia, the rust fungus, *Cronartium ribicola* J.C. Fisch., was introduced into Vancouver, British Columbia (BC) prior to 1914 (Güssow 1923). It spread rapidly throughout the province until about 1930, when annual surveys to document the spread within BC were discontinued because the fungus was common throughout the provincial range of western white pine (Mielke 1943). Incidence surveys in the 1940s (Buckland 1946; Thomas and Roff 1947) revealed extensive cankering to the point that western white pine was not economically worthwhile to manage. For many years regulations did not permit it to be counted as part of a successfully regenerated stand and it was cut down when young-growth stands were being spaced (pre-commercially thinned). Considerable blister rust research in BC has since demonstrated that wild stands can be successfully managed and new stands can be established from resistant parents that have been selected for seed orchards. This report is a synthesis of this research.

Natural pine infection

The orange aeciospores of blister rust produced on pines cannot infect pines directly, so the rust first must infect an alternate host (*Ribes* spp.). Generally, telia and basidiospores are produced on currants and gooseberries, the alternate hosts, when temperatures are less than 20°C (Van Arsdel et al. 1956). Field studies confirm that there is a reduction in the production of these spore types in eastern North America when temperatures exceed 20°C (Van Arsdel et al. 1961). In BC the basidiospores infect pines following wet weather or under dewy conditions. Because conditions in coastal BC are generally cool, pine infection may occur from May through to November, with most infections occurring during foggy days in September and October, and fewer infections occurring during hot, dry summer weather (Hunt and Jensen 2000). At higher elevations and in the interior of the province, the infection season is shorter. In the interior of BC the days are often too warm to favour basidiospore formation and there is less dew conducive to pine infection. However, thunderstorms and cool weather sometimes lead to successful infection prior to September, when most infection occurs (Hunt unpub.) There is also evidence that successful pine infection may sometimes occur at temperatures greater than 20°C in western North America (Bingham 1972). Annually, there are many potential infection episodes (probably approximately 30 – 60) at the BC coast (Hunt and Jensen 2000) and several in the interior.

After the germinating basidiospores penetrate the needle via the stomates, a coloured infection spot (yellow, red, orange or purple) does not become visible in the needle until the following spring. By fall the fungal pathogen enters the phloem of branches producing a 2 cm diameter mass of orange-coloured hyphae visible in the bark around the infected needle fascicle. However, if needle infection occurs by July, the infection mass may be visible in the bark by the fall of the infection year. Spermatia may form before winter, but usually develop the next spring and summer with flies transferring them among cankers (Hunt 1985). Compatible mating types result in aeciospores, which are usually released in late March or early April at the coast and late April or early May in the interior of BC. These spores can only infect leaves of currants and gooseberries. These leaf infections produce urediniospores or teliospores in 3 to 4 weeks. Urediniospores intensify the infection on *Ribes* spp., with more spore crops being produced where the

growing season is longest. Teliospores are produced in hair-like columns and each readily germinates to produce four basidiospores.

Pruning pines

In BC, most pine infections occur below breast height (Hunt 1982, 1998). If these infections are removed before they spread into the trunk, a stand of saw logs can be produced (Hunt 1982). Pruned western white pine is now counted as growing stock towards a successfully regenerated stand (free-to-grow). Lower branches should be pruned as soon as it is practical to do so (Hunt 1998). Sometimes needles attached to the main stem are removed by rubbing a gloved hand up the stem at the same time as branches are being removed. However, if there are high loads of inoculum coming from nearby *Ribes* spp., such as those growing in creek beds, or stand openings created by root disease, direct trunk infections or branch infections too close for pruning may occur at an early age, reducing the effectiveness of pruning (Hunt 2000). In these situations, seedlings can be physically protected from rust spores by placing solid deer protectors over them. When the saplings emerge from the protectors, the protectors should be removed only after the fall crop of basidiospores has been released, followed by pruning within two growing seasons (Hunt 2002a). Main stem cankers can be contained by scribing around them down to the wood if the distance from the visible orange canker margin is at least 1 cm, and the width of the scribe channel is at least 1 cm. At the top and bottom of the canker, the distance from the orange margin to the scribe channel should be at least 3 cm. In many cases such treatments girdle the tree (Hunt 1988b). Scribing around the bases of branches when branch cankers are within 10 cm of the main stem can be effective at preventing branch cankers from becoming established in the stem. Small trees (< 10 cm diameter) can be topped at the whorl below a main stem canker and the whorl pruned to permit one branch to become the new top.

Initiation of a resistance program

The above silvicultural controls add to the cost of growing western white pine. To reduce these costs, resistant seedlings can be planted. In 1983 the Canadian Forestry Service and the British Columbia Ministry of Forests signed a Memorandum of Understanding to develop blister rust resistant stock for BC (Meagher and Hunt 1985). What follows is a rationale for the selection of pine stocks used in BC and a discussion of the traits of the screened stock.

Target number of trees

In localized areas near *Ribes* spp. the number of cankers per tree can exceed 300 in BC. However, in natural stands the mean number of cankers per tree is about four (rarely up to 14) on 20- to 30-year-old trees (Hunt 1983). This suggests that phenotypically resistant trees, i.e., canker-free trees, may be found simply because they have never been inoculated rather than because they are genetically resistant. This would be particularly so in dense stands where it is difficult for spores to penetrate into the stand from outside inoculum sources (Hunt 1998). Meagher et al. (1990) estimated that about one canker-free tree in six might yield useful resistance, and if a seed orchard requires about 50 parents (Hunt et al. 1985) for a good population base, 300 trees would need to be tested. We initially had this target number for each of two provincial seed zones, coastal and interior, one zone for each of the two separate geographic ranges of western white pine in BC. Subsequent work (Meagher and Hunt 1998; 1999) re-affirmed the need for these two seed zones. Each zone was broken into geographic sections covering the range of western white pine. This breakdown was largely based on drainages and access, and then one-half the target was distributed among the geographic sections on an approximate equal area basis. This method allowed for good geographic sampling of western white

pine. The remaining 150 trees per zone were assigned later to geographic sections where it seemed that there were still many known white pine stands to survey, or where it seemed likely that canker-free candidates could be found. Candidates had to be of good form with equal or better growth than neighbours and, to reduce the chances of inbreeding, widely separated. The selected candidates frequently lacked cones and they had to be re-visited in subsequent years to have their cones bagged or scions collected. On subsequent visits some candidates were found to have become cankered and were then rejected.

Because most cankers are found below breast height (Hunt 1991), the candidates had to have all lower branches intact for examination. Insufficient candidates were located; thus the rules were relaxed to increase the number of candidates. Three new types of candidates were: canker-free trees without lower branches; trees showing no ill effects (tolerance) from a single basal canker; or trees with prominent bark reactions (Hunt and Meagher 1987) in the stem to one or more cankers (Hunt and Jensen 2001). To bring an end to the cycles of testing seedlings, candidate trees were not sought after 1991 and seed from candidate trees was not sought after 1993. At the coast, 318 candidates were located and 291 were tested; in the interior of BC, 307 candidates were located and 216 were tested (Meagher et al. 1995). In some years insufficient seed was available and seedlings were reared for inoculation from BC materials selected in the 1950s (Porter 1960), or the US Forest Service selected materials from Idaho and Washington states. When all geographically suitable trees were tallied (i.e., candidates, cankered trees, trees too close, and American trees), there were 378 coastal trees and 259 interior trees tested.

Seedling protocols and inoculations

Early screening programs for blister rust resistance screened ramets (grafted cuttings) from canker-free field selections (Porter 1960). However, Riker et al. (1949) and Patton (1961, 1967) showed that resistance could increase with age so that resistant ramets from mature trees often produced susceptible seedlings. Since most blister rust infections occur on seedlings and saplings, it is necessary to have resistance in young stock in order to produce a mature white pine crop. During the summer, candidate trees for testing were examined for cones and, if present, 5 to 10 were bagged in cloth-meshed bags. This helped protect the seeds from squirrels, as well as providing bags of seed that could be retrieved over several months (rather than guessing when cones were mature enough for picking). Seed was extracted in the fall, inventoried and stored at about 0°C. The seedlings produced from these seeds were regarded as half-sibs because there was no control over pollination.

Hoff and McDonald (1980a) published a protocol for growing and inoculating seedlings in Idaho. The BC programs followed this protocol with a few adjustments (Hunt 1988a). These included removing the very susceptible primary needles from 2-year-old seedlings by hand. Because our seedlings were grown in styroblocks, they could be moved to comfortable locations for observations, as opposed to the Idaho method of crawling on the ground examining seedlings in beds. The styroblocks had 45 cavities (340 ml each), and in the first 3 inoculation years, five families of nine half-sibs per block were transplanted into these blocks and in later years, nine families of five half sibs were used. Ninety half-sib seedlings per family were inoculated in a randomized design. To keep the seedlings in these styroblocks for two growing seasons, they had to be kept small to minimize losses from *Botrytis* (gray mould). To accomplish this, seedlings were sown late (about mid April) into styroblocks with 160 or 198 cavities each (60 ml each) and transplanted to the blocks with 45 cavities for the second growing season. After the second growing season the 2-year-old seedlings were inoculated and maintained in the styroblocks for their third growing season. Good airflow to minimize *Botrytis* infection after the second year was aided by the removal of live and dead primary needles. After their third growing season, cankered seedlings were grown in beds and canker-free seedlings were grown in 4-litre pots. However, to reduce the mortality caused by poor water distribution in these pots, future studies will use styroblock cavities with a volume of 1000 ml.

Ribes leaves infected with *C. ribicola* from an inoculated *R. nigrum* L. garden or selected groves of inoculated *R. bracteosum* Doug. were picked for pine inoculum when copious telial columns appeared as if they had icing sugar on them (an indication that they were germinating to produce basidiospores). This usually occurred following the first rain in September. Inoculation occurred in a seedling storage locker which prevented drafts, and maintained temperatures below 20°C. The *Ribes* leaves were placed on wire screens 60 cm above the seedling canopy, a height from which the basidiospores would be somewhat dispersed rather than being clumped. To minimize atypical germination of basidiospores (Hansen and Patton 1975) only small water droplets were produced on the seedlings. We could accomplish this only by hand-misting with electric misters. *Ribes* leaves were also hand-misted. To maintain a high humidity around the seedlings, they were placed in large boxes with about 5 cm of water in the bottom and shrouded with wet foam sheets over the *Ribes* leaves. The sides and ends were covered with wet burlap hung from a wire support into the water below. Spore casting ceased at 3000 spores/cm^2, which was usually accomplished in one or two nights. This control over air movement and inoculum density meant that pine families could be compared for relative infection severity. The seedlings were maintained with small droplets under high humidity conditions at less than 20°C and under sodium vapour lights for 8 or more hours following spore casting. This was thought to assure open stomates and optimal conditions for *C. ribicola* penetration. About 60 families per year were inoculated in this fashion from 1987 through 1995.

Selecting for rust resistance

Initially, the BC selection program followed Hoff and McDonald's (1980a) protocol to observe resistance responses. These responses included: 1) seedlings lacking infection spots; 2) families with reduced infection spotting; 3) seedlings shedding infected needles; 4) spotted seedlings lacking cankers; 5) seedlings with bark reactions; and 6) seedlings with slowly growing cankers.

Family trait – few infection spots

Hoff and McDonald (1980a) suggested that families with few infection spots were more resistant than families with many infection spots i.e., their relative infection severity would be less. To compare families they used an infection unit of 1 linear metre of needle. By counting infection spots on two upper needle fascicles and measuring the length of their needles they calculated the infection severity on this unit. We agreed with their premise, but not their methods. They did not demonstrate that the upper two needle fascicles were representative of the infection spotting on a seedling; it seemed likely that these needles would be more exposed and intercept more spores than lower needles. Thus, we counted all infection spots per seedling. Because we market trees and frequently measure mortality in numbers of dead trees, we used the seedling as the infection unit, rather than a metre of needle. From infection spots per seedling we could calculate mean infection spots per family. Infection spots were tallied by well-supervised students usually over one weekend in early May. Once the infection spotting data were gathered, Hoff and McDonald (1980a, b) did not provide a method to classify families into high and low infection classes. We used two methods. One was the Student-Newmans-Keuls multiple range test. However, the variance was always high and families were rarely separated unless the over-all family spot mean was used instead of the mean of the means of the styroblock row plots (Hunt 2002b). The other method was to convert the family means to percentiles, which permitted families inoculated in different years to be similarly grouped and compared (Hunt 2003a). An arbitrary cut-off, such as the least spotted 1/6 of the families, could be selected as the least spotted families.

Unfortunately, there was no correlation between family mean spotting and mean cankering in plantations (Hunt 2002b; Fig. 1). Frequently, the spotting on a seedling appeared random, but in a few situations needles from the same bundle had infection spots at the same position or positions along the needle, and

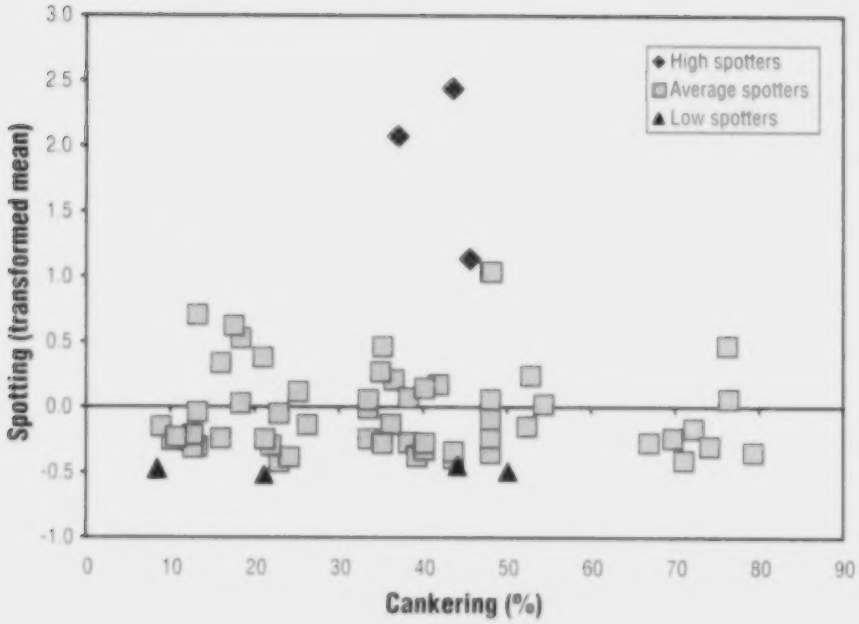

Figure 1. Several families of western white pine with average needle infection spot values (as determined from inoculations) had more cankered individuals in a plantation than highly spotted families. Four families with significantly lower infection spotting values than three other families with significantly greater infection spotting values, overlapped in field cankering incidence. All field trees were subjected to only natural inoculum and classified as cankered or canker-free.

sometimes needles from adjacent bundles had infection spots close to these same positions, suggesting that particular locations on needles are more susceptible than other locations. Additionally, it is the current needles that are inoculated in screening trials, but on older seedlings and trees in the field these needles are much less susceptible than 1-year-old needles (Buchanan 1940; Bedwell and Childs 1943; Hunt and Jensen 2000; Hunt unpub.) The family rank based on spot counts on current needles was strongly inherited (Hoff and McDonald 1980b; Meagher and Hunt 1996; Hunt 2003a), but the field data suggest that they are unlikely to correlate to spotting on older needles and subsequent field cankering. As a result, counting spots and calculating family mean spotting values of 2-year-old seedlings is not worthwhile. This means that inoculum dosage does not need to be critically controlled, and consequently the time involved in monitoring *Ribes* bushes for basidiospores production, picking leaves, and setting up an inoculation chamber can be eliminated. Seedlings for inoculation can be put under infected *Ribes* bushes and left for natural inoculation, which occurs readily at the coast in BC. Future inoculations of crosses among resistant pines (King and Hunt 2004) will assure that seedlings are spotted, but it will not be necessary to count all infection spots.

Seedling trait – needle shed

McDonald and Hoff (1970) observed that some seedlings bore infected needles in the spring following inoculation, but that they were cast during the summer and thus no infection spots remained by the fall. The seedlings did not develop cankers over the next 2 years. Although McDonald and Hoff (1971) did

not strengthen the hypothesis that needle shedding had a genetic basis by reconfirming the phenotype by re-inoculation, they did attribute this phenomenon to a recessive gene. In our first successful inoculation we had some needle shedding caused by *Botrytis*, but three seedlings appeared to possess legitimate needle shedding resistance. These were cloned and all became cankered on re-inoculation. With *Botrytis* under control, needle shedding was rarely observed and when it did occur, both spotted and healthy needles were shed. No resistance was associated with any needle shedding. Hoff et al. (1973; Hoff and McDonald 1980a) calculated 40 to 47% of the seedlings derived from the R.T. Bingham (Idaho) seed orchard would be canker-free because of the needle shedding trait. This is a good seed source for the interior of BC because it has little rust, but at the coast it is severely cankered (Hunt and Meagher 1989; Hunt 2004). Further work at the coast and in the interior with seedlings derived from the R.T. Bingham seed orchard confirmed that needle shedding was caused by stress such as drought, not by a genetic trait conferring resistance to blister rust (Hunt 2004). If this seed source is inoculated early in the interior of BC, then seedlings can be severely cankered, but resistance likely increases with age, making it an effective seed source for much of the interior (Hunt 2004).

Seedling trait – Fungicidal short shoot

Hoff and McDonald (1971) observed that some seedlings were spotted but canker-free 18 months post-inoculation. They attributed this to a resistant trait controlled by another recessive gene, which was activated in the "short shoot" of the needle fascicle, thus the name "fungicidal short shoot". Again, Hoff et al. (1973; Hoff and McDonald 1980a) calculated that 10 to 12% of the seedlings derived from the R.T. Bingham seed orchard would be canker-free because of this trait. They did not re-inoculate the phenotype to strengthen the hypothesis that the fungicidal short shoot resistance had a genetic basis. In our coastal inoculations we too observed that seedlings can be spotted and canker-free 18 months post-inoculation, but if observed longer all spotted seedlings became cankered. Perhaps fungicidal short shoot resistance works only in the interior of BC, and this might partially explain why the R.T. Bingham seed orchard source performs well in the interior (Hunt and Meagher 1989; Hunt 2004). However, when we later raised seedlings from the R.T. Bingham seed source in the interior, and inoculated them there (from 1998 to 2002) (Hunt 2004) we never observed a fungicidal short shoot response. What we did observe was that where the winter was longer (e.g., near Salmon Arm; see Fig. 2) than at the coast, the pathogen seems delayed in reaching the stem or branch and when it does, more slow-canker-growth resistance may ensue. Where the winter was even longer (e.g., near Nelson; see Fig. 2) needles might be spotted for a few years and then abscise naturally before the fungus has a chance to grow into the branch or stem, thus less slow-canker-growth resistance was observed. Even this "spots only" observation occurred in very few seedlings. There appears to be a similar south to north trend in plantations established with R.T. Bingham orchard seed source, with some saplings in southern Idaho displaying slow-canker-growth resistance, whereas they are canker-free in BC where the growing season is shorter (Hunt 2004). There is a correlation between a shorter growing season and elevated quantities of general defence proteins (such as PR 10, which is induced by winter conditions, Ekramoddoullah et al. 1998; Yu et al. 2000), which are then available to inhibit the growth of the blister rust pathogen over a longer time-frame than where the growing season is longer and these inhibiting proteins are at low concentrations. This environmental influence on a generalized defence response may partially explain why the R.T. Bingham orchard seed source does well in the BC interior, but not at the coast.

Seedling trait – bark reactions

The term "bark reaction" seems to have a different definition with each blister rust worker (Hunt 1997). Here, the term is restricted to small reactions in the stem that are centred around needle fascicles and occur when the first cankers are observed (i.e., 15 to 18 months post-inoculation). It appeared to be a reaction in

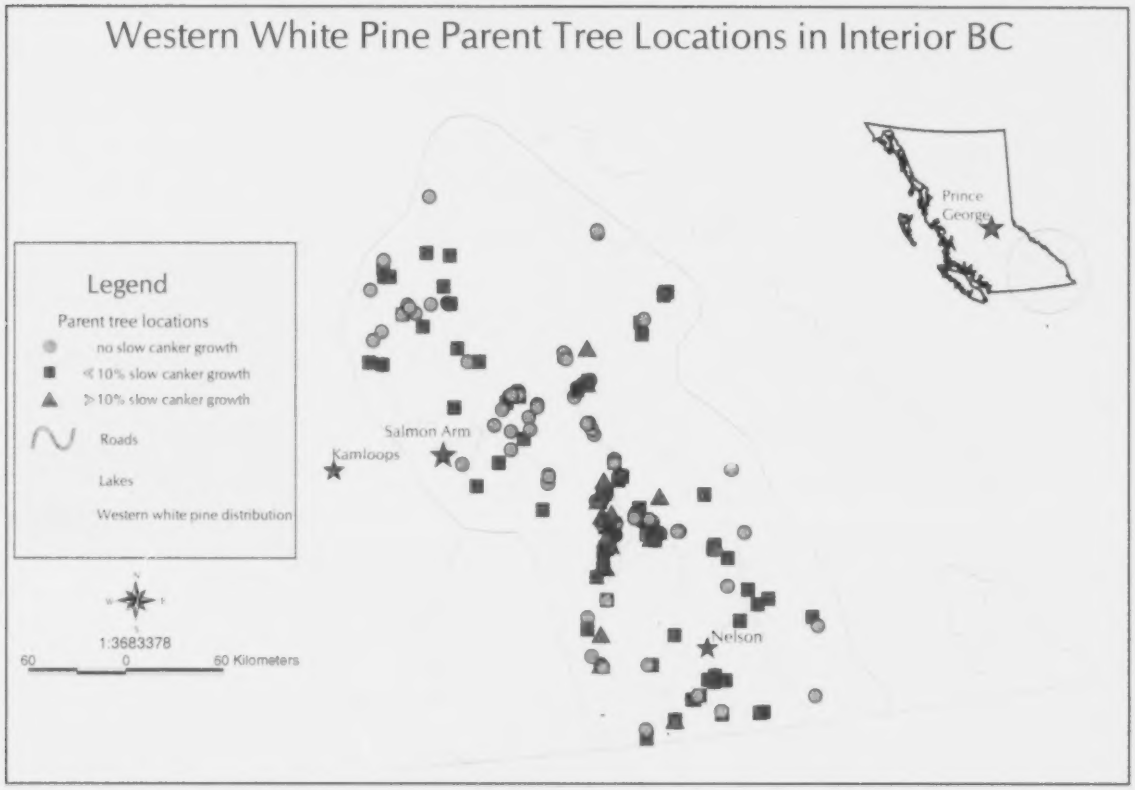

Figure 2. The distribution of slow-canker-growth resistance in sampled western white pines from the British Columbia interior. Note locations for Salmon Arm, Nelson, Kamloops and Prince George.

the periderm (bark), but this needs confirmation. Often these were circular (Fig. 3). From the 1987 and 1988 inoculations, 45 seedlings with these responses were cloned. There was no apparent family pattern to these bark reactions. After the second inoculation the bark reaction phenotype was repeatable in only Porter's (1960) D1 clone. This clone was later determined as a *P. strobus* L. rather than a *P. monticola* (Hunt et al. 1990). Various fungi were isolated from these "bark reactions" and sometimes *C. ribicola* emerged and killed the seedling, or the seedling was killed by normal *C. ribicola* cankers elsewhere on the stem. *Phoma herbarum* Westend. was common among these secondary fungi and, even when it was inoculated alone, the phenotype could be repeated (Hunt 1997). Similar phenotypes were produced by *Botrytis* sp. infection of seedlings and *Mycosphaerella pini* Rost. in Munk in the field. At the US Forest Service testing facility in Dorena, Oregon, some of these bark reactions do show a family pattern in inoculated western white pine seedlings (Sneizko and Kegley 2003), and thus are likely to be the result of a host response to *C. ribicola*. However, in BC these are considered to be exceedingly rare, and all such seedlings were treated as cankered, or re-inoculated. Before flushing as 4-year-old seedlings (15 to 18 months post-inoculation) all cankered seedlings (including those with "bark reactions") were removed from styroblocks and placed in cull beds. Two to 3 years later, survivors were examined for bark reactions and slow-canker-growth responses. No bark reaction seedlings came from the cull beds. At 15 to 18 months post-inoculation, all healthy trees were potted into 4-liter containers. Of these, 10 coastal seedlings were eventually classified as having bark reactions and cloned for seed orchards. No interior seedlings were classified as having bark reactions.

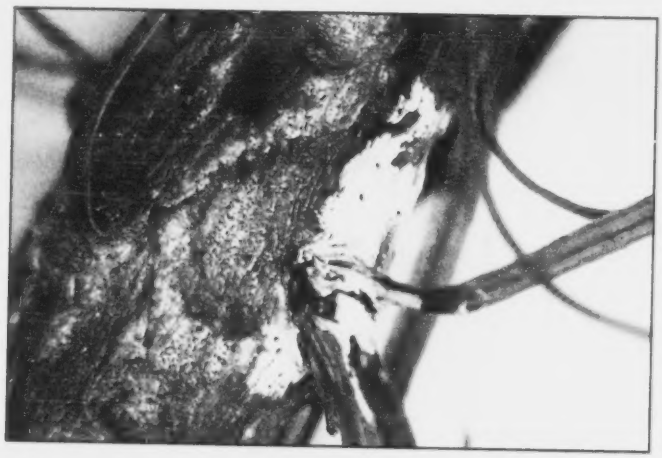

Figure 3. Several different fungi, including *Cronartium ribicola*, caused a circular bark reaction at the base of a needle fascicle on a western white pine stem.

Seedling trait – difficult to infect (DI)

During spring spot counting after a fall inoculation, some seedlings had zero infection spots while spotted seedlings surrounded them in the styroblock. Hoff and McDonald (1980a) consider this to be a resistant trait called "no spots". Unfortunately, they never re-inoculated such seedlings to confirm that the phenotype was likely to be caused by a genotype. From the 1987 and 1988 inoculations, 69 such seedlings were cloned and re-inoculated. Most ramets became cankered, often with several cankers. No clone was canker-free, but one clone had four canker-free ramets and one ramet had a single branch canker. We called this seedling "DI" for "difficult to infect". We called the original unspotted phenotypes "spots zero". Thereafter, we retained DI seedlings from re-inoculated seedlings (spots zero seedlings and any others that failed to develop a canker 3 to 4 years post-inoculation) if they had three or less cankers, while most spots zero seedlings were severely cankered and rejected from the program. For the coast, 106 families (28% of those tested) produced one or more DI seedlings, and for the BC interior 26 families (10% of those tested) produced one or more DI seedlings. Patton (1961; 1967) demonstrated that as eastern white pine trees age, more of the penetrating spores fail to produce invasive secondary hyphae. A very similar ontogenic resistance has been reported for grapes against mildew (Ficke et al. 2002) and similar ontogenic, or "mature plant" resistances are well known against other rust fungi (Heath 1982). Likewise, DI resistance may be a trait in seedlings that causes many of the penetrating spores to be unsuccessful. If so, it seems likely that this trait will increase within a family as the family ages. This would make these families more successful on low hazard sites, or where deer protectors are used to permit the resistance to increase with age.

Seedling trait – slow-canker growth (SCG)

Diamond-shaped cankers with prominent orange margins (about 2 cm long) girdled the stems 16 to 24 months post-inoculation on normal susceptible seedlings. Slowly growing cankers usually appeared at 36+ months. We recognized four types of slow-canker-growth resistance (SCG) (Hunt 1997), all with small (<2 mm) or no visible orange margins, and the pathogen usually extended beyond the periderm into the cambium; thus, it was more than a "bark reaction" (Jensen and Hunt, unpub.). The fusiform type (Fig. 4)

resembled a normal canker, but because it grew slowly it may be only on one side of the stem. The constricted type (Fig. 5) was often resin soaked and girdling the stem, sometimes causing the stem to snap at the canker. The gall type (Fig. 6) resembled a western gall rust canker and sometimes, after 2 or 3 years, the pathogen grew at a normal rate. The no-swelling type (Figs. 7 and 8) was considered the best of the four because it was small and irregular, and often healed completely. The categories were not absolute, and designations sometimes changed from one observation to the next. Re-inoculation of seedlings displaying the no-swelling type of resistance reproduced the same phenotype; the galled-type on re-inoculation was sometimes normally cankered. All but the constricted type sometimes produced a few aeciospores. In the field, because most rust cankers were initiated on branches, these types of cankers were not likely to reach the stem, or if initiated in the stem they would have difficulty girdling it. For the coast of BC, 200 families (53% of those tested) produced some offspring with SCG, and for the interior 109 families (42% of those tested) produced SCG offspring. Three population samples and a control family from a cankered tree, which was used in all inoculations, did not produce any slow-canker-growth seedlings. The resistant families were well distributed throughout the province (Figs. 2 and 9). Among western white pine in the interior of BC, seven families had >20% incidence, with one family as high as 41.5%, and for the coast, three families had >20% incidence of SCG. These proportions lead us to expect that seed orchards composed of SCG resistant individuals will produce offspring with >40% SCG resistance.

Figure 4. The fusiform type of slow-canker-growth resistance to *Cronartium ribicola* in western white pine. Note the leading edge of the canker is the typical diamond-shape as found in normal cankers, but lacks the prominent orange margin caused by masses of pathogen hyphae.

Figure 5. The constricted type of slow-canker-growth resistance to *Cronartium ribicola* in western white pine. Several constricted cankers are resin-soaked and the seedling may break at the constriction.

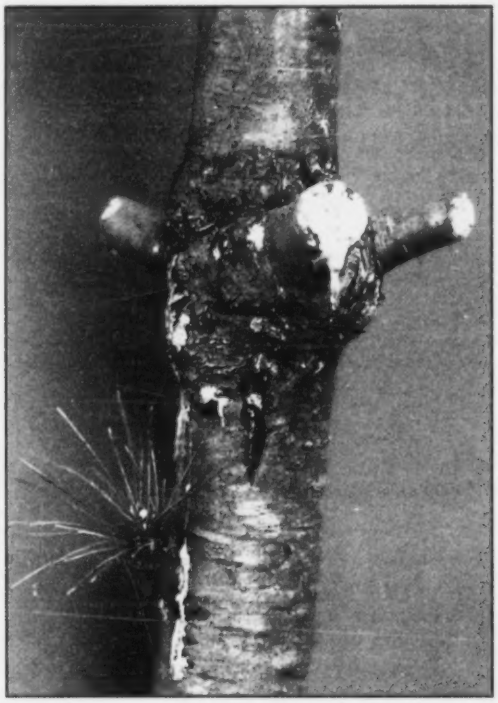

Figure 6. The gall type of slow-canker-growth resistance to *Cronartium ribicola* in western white pine.

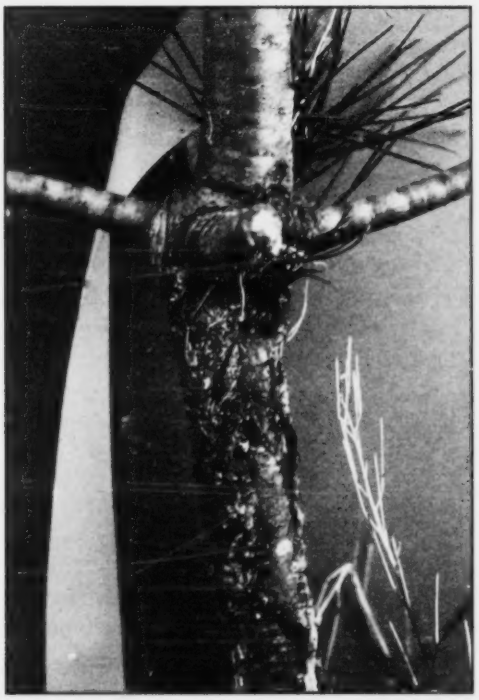

Figure 7. The no-swelling type of slow-canker-growth resistance to *Cronartium ribicola* in western white pine. Note the irregular canker margin.

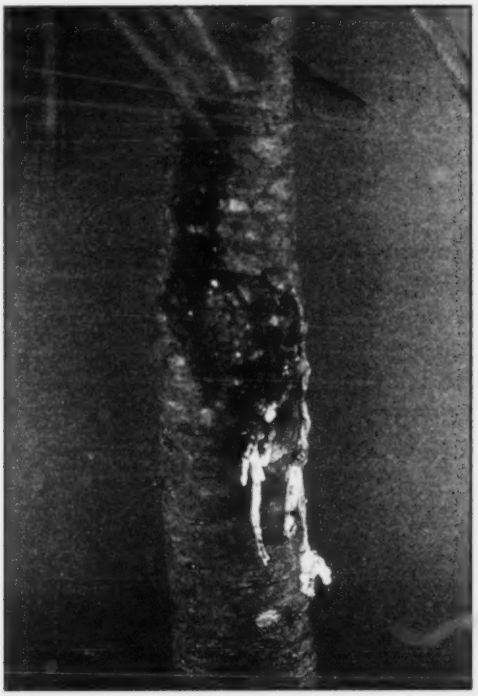

Figure 8. The no-swelling type of slow-canker-growth resistance to *Cronartium ribicola* in western white pine. These small cankers may heal entirely, leaving no trace of infection after a few years.

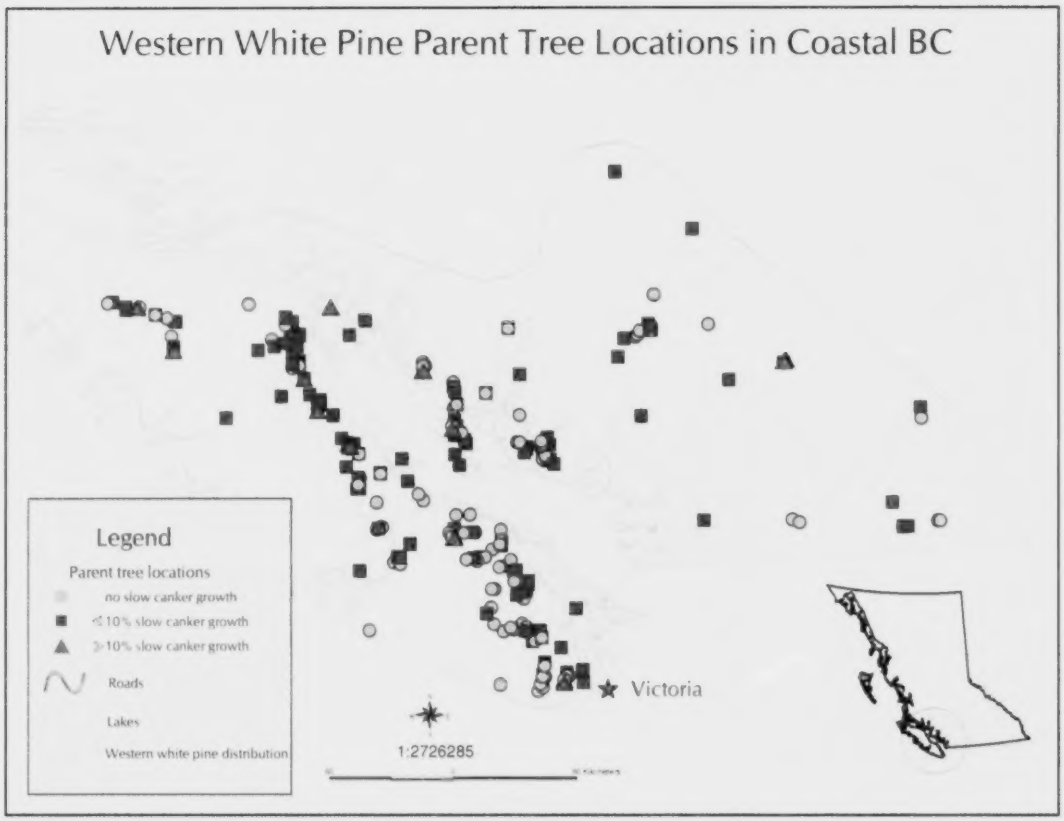

Figure 9. The distribution of slow-canker-growth resistance in sampled western white pines from coastal British Columbia.

Frequently, families produced both SCG and DI seedlings (Table 1). Over 75% of the DI resistance in coastal families was identified in SCG families, and the percentage was over 69 for the interior of BC. Sometimes both traits were found in the same seedling. The mean number of DI seedlings per SCG family was 2.2, and for other families it was 1.6. These numbers would suggest that seed orchards composed of SCG individuals would have additional resistance because of DI. It seems possible that seedlings in the same family with DI and SCG resistance are displaying different forms of the same ontogenic resistance, so seedlings could lack cankers, have few cankers, or display various forms of SCG. As these families age, it seems plausible that there is a shift towards less development of secondary hyphae by *C. ribicola* spores, and if penetrations ramify further, they may result in SCG responses. This would explain why families with little SCG resistance had good field resistance (Hunt 2002b). If this is also the resistance predominant in the R.T. Bingham seed orchard, then the greater susceptibility of the southern plantations compared to northern

Table 1. Number of difficult to infect (DI) resistance families and individuals in inoculated slow-canker-growth (SCG) resistant western white pine from the two seed zones in BC.

	SCG		non SCG	
	Families	Individuals	Families	Individuals
Coastal zone	80	187	26	46
Interior zone	18	27	8	8

plantations (Schwandt and Ferguson 2003; Hunt 2004) can be similarly explained (i.e., in southern plantations successful development of secondary hyphae from penetrating spores causes more frequent SCG responses, while in the more northern plantations there is less frequent development of secondary hyphae from penetrating spores so there are fewer SCG responses and more canker-free trees). There would be some variation depending on stand age. For instance, when evaluating the R.T. Bingham seed orchard seed source, Schwandt and Ferguson (2003) reported a greater incidence in SCG ("bark reactions") responses in young plantations than Hoff et al. (1973) reported from seedling inoculations. Also, the young plantations in southern Idaho may appear fully susceptible if infected shortly after establishment. This concept is further supported by inoculation of clones derived from parents that produced a high incidence of SCG offspring. Incubation of inoculated clones at a low elevation site resulted in more infection and more SCG responses than at a high elevation site (Hunt unpub.). Also, Sniezko and Kegley (2003) reported similar observations of inoculated seedlings when they described "Mechanism Q" as a family trait with canker-free individuals being of relatively high incidence in SCG ("bark reaction") families.

R gene resistance

R genes are dominant genes for resistance that are usually found in the heterozygous condition, i.e., open pollinated seed collected from such an individual would simply segregate 1:1 with approximately one-half of the offspring being canker-free and the other half being normally cankered. In all our screening tests we have never observed any such segregations from BC collections. Most R genes produce a "hypersensitive response", i.e., the pathogen penetrates its host but the first invaded cells respond quickly, confining the pathogen to a small necrotic spot. The first white pine R gene, designated Cr1, was reported to cause a hypersensitive needle spot in sugar pine (Kinloch and Comstock 1981) and the second, Cr2, in western white pine from Oregon (Kinloch et al. 2003). Ontogenic resistance is generally considered to be complexly inherited and to be a durable form of resistance (Hunt 2003b), whereas, with R genes the pathogen usually has a simple matching gene that overcomes the R gene. In Oregon, the trees first found with the Cr2 gene were reported cankered about 40 years after the introduction of rust. Offspring of these Oregon trees have been planted in BC at several locations since 1987, and to date the Cr2 gene appears to be holding. Repeated intense inoculation with BC inoculum of seedlings having Cr2 has failed to overcome the Cr2 gene (Hunt et al. 2004). In BC one other putative R gene has been identified in Oregon-derived stock, but this gene has failed on some sites (Hunt 2002c). Other putative R genes have been identified in Oregon (Sneizko and Kegley 2003). These genes are best used in tandem or pyramided, as one gene will tend to protect the other. They may be used singly for a short time and monitored in case silvicultural intervention becomes necessary. Such imported genes also may bring undesirable traits, such as poor growth (Meagher and Hunt 1998) or susceptibility to other pests. Adding R genes to ontogenic resistance trees should provide excellent resistance.

Seed transfer

Western white pines in the Pacific Northwest are diverse within populations, but rather similar among populations (Hunt and von Rudloff 1977; Steinhoff et al. 1983; Rehfedt 1984; White 1991), perhaps because they dispersed after the last ice age from a common gene pool (Critchfield 1984). This has resulted in broad seed transfer zones. Within BC, coastal provenances were not has hardy as interior provenances (Thomas and Lester 1992). Height growth was inferior in the interior whereas, at the coast, interior provenances grew well (Meagher and Hunt 1998). Interior provenances, particularly those from the south (King and Hunt 2004), can then be used at the coast, but coastal provenances should be restricted to the coast. Because of their rust susceptibility, resistant selections from Idaho are not recommended for transfer to the coast, but they are recommended for the interior (King and Hunt 2004). Movement of Idaho stock into the northern range of western white pine in BC is not recommended because it appeared to suffer more frost

damage than local stock (Meagher and Hunt 1999). Most of the interior SCG selections are from southern BC (Fig. 9) and they, too, may need to be used with caution in the northern part of the range (the species ranges over 4° latitude in BC). However, beyond the range of western white pine, the R.T. Bingham seed orchard-derived stock grows well on a southern exposure in the Cariboo (north of Kamloops, Fig. 2). More testing in the northern part of the species range and at higher elevations may suggest that additional selections be made to avoid environmental damage for reforestation in the northern range of western white pine. Although planted western white pine can grow as far north as Prince George (Fig. 2), it only grows well on southern exposures. Western white pine has potential use on certain sites north of its traditional range, and the large internal population variation suggests that clones could be selected for use farther north on a variety of sites.

Similarly at the coast, populations from southern Oregon grew (on a statistical basis) at the same rate as local populations, but they ranked low for height growth over several sites (Meagher and Hunt 1998). On this basis, it was recommended that no direct transfer be made from south of the Columbia River. Southern Oregon trees bearing the Cr2 gene crossed with trees from Washington State grew well in BC.

Conclusions

Resistance in native western white pine is ontogenic, i.e., it increases with plant development and is influenced by environmental factors. We recognized two forms which may be related: DI for "difficult to infect seedlings" and SCG for "slow-canker-growth resistance". Surprizingly, about one-half of the trees tested produced seedlings with 1% or more of their seedlings displaying SCG resistance, and 32% of these families displayed DI resistance, while 5% of families displayed only DI. These families are well dispersed in BC (Figs. 2 and 9). Two seed zones are recognized: coastal and interior. Idaho trees can be grown successfully in the BC interior, but further testing of these and southern BC pines needs to be done at northern latitudes and high elevations to be confident of their use in these locations.

Single resistance genes (i.e., R genes) seem to be lacking in BC populations, but they can be imported from American western white pines and used in breeding programs. These pines largely originate in coastal populations south of the Columbia River. They do not perform as well as pines originating north of the Columbia River and thus are not recommended for direct use in BC.

To date there are three resistant western white pine seed orchards in coastal BC and one in the interior, all using scion material. One coastal orchard uses DI and SCG identified seedlings; one uses these plus "needle shed", "spots zero" and Oregon selections, and one uses the parents of DI, SCG, and reduced spotted families plus mature selections from Oregon. The interior orchard has DI and SCG identified seedlings interspersed with mature selections from Idaho. The advantage of using parental scions and mature tree scions is that pollen and conelets are produced early for breeding and seeding purposes. Plantations have been established recently to test for relative blister rust resistance and growth performance among the different resistant types currently growing in the orchards. Also, blister rust testing of full-sib crosses among orchard selections (King and Hunt 2004) has been initiated.

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